

RARE SPECIES OF PLANTS

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WHAT IS RARITY?

Rarity implies both a relative quantity and a quality, that is, both biological and human aspects. In general people ascribe higher value to a rare item, and most people expect that a rare species will have qualities of elegance. The Whooping Crane (*Grus americana*), and Quetzal (*Pharomachrus mocino*), Cheetah (*Acinonyx jubatus*), and Sable Antelope (*Hippotragus niger*) fulfill this expectation. Some species project a feeling of the dramatic and thus assume an aspect of importance. Eagles, such as Golden Eagle (*Aquila chrysaetos*) and Bald eagle (*Haliaeetus leucocephalus*) do this. One occasionally comes on a few Cardinal Flowers (*Lobelia cardinalis*) blazing in a shaft of sunlight against deeply shaded woods. Species which occur in distant places, Polar Bears (*Thalarctos maritimus*) and Big Brown Bears (*Ursus arctos ssp. middendorffi*), seem more likely to be considered rare and thus preferable than are ones with which people are familiar. Consider the traditional use in rock gardens of Alpine wildflowers from Switzerland rather than those from the mountains of New England.

Yet, the Cape Sable Seaside Sparrow (*Ammospiza [maritima] mirabilis*), an undistinguished "little brown bird" of questionable species qualifications, is accorded rarity status and "an Endangered Species" status. So, in the Gulf of Maine a small and relatively isolated population of Atlantic Puffins (*Fratercula arctica*) and so in Britain, a small and relatively isolated population of Leach's Petrel (*Oceanodroma leucorhoa*) are considered rare even though these two are among the most abundant species of birds in the world. It could well be a source of puzzlement to the botanists who know the plants in the fullness of their abundance across the tundra and coniferous forests of North America to know that each stand of Labrador Tea (*Ledum [decumbens] groenlandicum*) is catalogued in Massachusetts, and a careful search is made in Maine for stands of Jack Pine (*Pinus Banksiana*), of Shrubby Cinquefoil (*Potentilla fruticosa*), and of Baked-apple Berry (*Rubus Chamaemorus*).

Thus, the human standards by which the status of rarity is conferred are complex and to some degree contradictory.

Is Rarity Failure?

There is an old idea that rare species are failing species; that a rare species lacks the ability to displace other species, to increase its population, or to expand its range.

Some species have strong attachments to traditional range and are reluctant to colonize new or even former range once it has been abandoned. Such a species group is that of the Bighorn Sheep (*Ovis canadensis* and *O. dalli*) which, although widespread at present, is like the domestic sheep, resistant to occupying unfamiliar range (Geist, 1967, 1971) and are, as it were, preadapted to rarity. Many seabirds are similarly conservative (Lack, 1967).

Oddly, there are geographic regions where "conservative" species cluster: Newfoundland in northeast North America and the lands surrounding the Bering Sea in the northwest. In these centers of high species diversity, species of limited geographic ranges are apparently able to displace the widespread "successful" species. So they do quite well on their own sites even in the face of intense competition.

The idea that rare species are failing perhaps results from observations that many rare species occur in isolated patches in mountains, bogs, sand dunes, or islands. This idea is strengthened by traditional projections by students of climate that Arctic-Alpine plants once had continuous distribution around the borders of the ice sheets and have subsequently retreated to bogs and mountain tops. The idea is also reinforced by classical geological doctrines that beaches, mountain tops, and bogs are temporary features, doomed to disappear. Some botanists seeking to explain patterns of species diversity noted that conservative species were found in areas believed to have been islands in a sea of ice during the ice advances (Fernald, 1924, 1925; Hultén, 1937).

There is also an old idea that species run a cycle from youthful aggressiveness to mature vigor and declining powers in old age. Willis' (1922) "Age and Area" hypothesis suggested that a species begins with a small population and expands with age. Fernald's (1925, 1929, 1931) suggestion of "senescent" species in the Gaspé-Newfoundland region caught the imagination of his peers when his previous "common-sense" explanations received little notice. Ricklefs and Cox (1972) used the concept of a species cycle in their description of a sequence of bird species of West Indies islands. They suggested that a species, following colonization, rapidly spread into diversified habitat. Then as subsequent species arrived,

the older colonists became progressively more restricted in distribution and specialized in habitat, because the older residents, unable to match the competitive abilities of later colonists, had their wider habitats preempted. This description fits attractively with theories which use rates of colonization and extinction to explain the number of species on islands (MacArthur & Wilson, 1963, 1967). Lack (1973), criticizing what he considered to be the too general application of the colonization/extinction model, suggested the opposite for some observed cases in hummingbirds in the West Indies. He suggested that later arrivals were unable to become established because their niche was already occupied. Numerous instances of this can be found among plants (Polunin, 1960).

Definition of Rarity

If rarity is measured in terms of numerical relation to other sympatric species, it appears that most species of plants and animals are rare. Of a regional list of a hundred species, we can expect a dozen to be common and widespread, and usually the rest will occur in smaller numbers. In general, the larger the area sampled as one community type the larger the list of species found in small numbers, while the roster of common or "important" species does not increase.

Abundance generally is considered to be made up of three aspects: frequency, consistency, and density. All three affect our recognition of rarity or commonness. Frequency is defined: "If sample plots are distributed throughout an area. . . and the number of plots in which each species occurs is recorded. . . frequency expresses the percentage of sample plots in which a given species occurs." Consistency reflects regularity of occurrence in samples, and density reflects number of individuals per unit of area (Phillips, 1959). The spectrum of frequency appears to be continuous down to some extreme cases of very rare species (Raunkaier, 1918, 1934). Gleason (1920, 1929) and Preston (1948, 1962) showed that the distribution of commonness and rareness follows an exponential or "log-normal" curve.

If we consider only the number of individuals, a "Poisson distribution" of commonness and rarity appears. A few species such as Sugar Maple (*Acer saccharum*), or White Spruce (*Picea glauca*), or Haircap Moss (*Polytrichum commune*) occupy one limit of the distribution. They are conspicuously abundant and widespread "primary or dominant species." At the other end of the curve, a few

species are conspicuously rare and endangered. In between, the large number of "secondary" inconspicuous and infrequent species occupies the bulk of the "normal" curve. Many papers were published on this general subject during the 1960s, largely in response to stimulation of MacArthur's work (1957, 1960). These studies were not really directed at the questions considered here. It seems prudent to start with a definition that does not imply quality or success until we know what these words mean and what they imply.

An operational definition of a rare species might include the characteristics that it either occurs in widely separated, small sub-populations so that interbreeding among sub-populations is seriously reduced or eliminated, or is restricted to a single population. One would expect that there are several "kinds" of rare species as well as several kinds of historical sequences, several selective mechanisms, or several habitat characteristics by which they are produced.

Types of Rarity

Mayr (1963) suggested three main types of geographic distributions of rare species, acknowledging that there is a spectrum of intermediate types. First, the range of some species is restricted to a very few localities, and they are considered rare even though they are found in large numbers at each locality: for example, Mountain Avens (*Geum Peckii*), which grows in the alpine zone of the Presidential Range of New Hampshire, or Abbott's Booby (*Sula abbotti*) of the Indian Ocean. Such a distribution of the breeding population does not necessarily guarantee recognition of rarity for a highly mobile species. Alaska Fur Seals (*Callorhinus ursinus*), breeding on the Provilof and Commander Islands, and Greater Shearwaters (*Puffinus gravis*), breeding on three islands in the South Atlantic, are not considered rare. The reason is, I presume, that both spread widely over the oceans in the non-breeding season and are seen commonly on their wintering grounds.

Secondly, some species are found in very small numbers widely dispersed in each community where they grow, but they occur in many suitable areas over their geographic range. Many orchids, gentians and saxifrages, as well as Peregrine Falcons (*Falco peregrinus*) have this sort of widely dispersed distribution. These make satisfactory quarry for those who are interested in finding rare species.

Thirdly, some species occur as a very few individuals or small groups at widely scattered localities over a large geographic area of what appears to be suitable habitat: for example, the alder, *Alnus maritima*, or Bachman's Warbler (*Vermivora bachmanii*) in the southeastern United States. A number of ferns and raptors have this kind of distribution.

1. *The range of some species is restricted to isolated localities yet they occur in large numbers at each locality.* Many island sites are large enough and remain reasonably homogeneous and consistent over time to supply uniform suitable and dependable sites. An important aspect of success on such places is "sticking with a good thing" once one has it. The widespread development of loyalty to a breeding site (*Ortstreue*) among migratory birds in general and seabirds (Lack, 1967) in particular suggests that return to a locality at which parents were successful can be used to "predict" breeding success. Put in other terms: if one was successful at one site, one does better to repeat the effort at that site rather than risking an attempt at a new site.

Once a population is successful on an "island" the possibility arises that dispersal will be "too expensive", because too large a percentage of dispersing individuals perish. Thus Lindroth (1957, 1963) showed that beetle populations on islands tend to have a large proportion of wingless forms. Flightless rails on oceanic islands provide conspicuous illustration. Carlquist (1971) showed that a similar suppression of dispersal mechanisms has occurred among Beggar's Ticks (*Bidens*) on the islands of the Hawaiian chain. The hazards of this commitment to the *status quo* is illustrated by the demise of the flightless Great Auk (*Alca impennis*) while its flying close relative survived, the Razorbill (*Alca torda*).

Recent studies of isolated populations of plants and animals on mountainous or oceanic islands indicate that there are rapid and often extensive changes in species composition. The size and geographical structure of an island has an important influence on the number of species in the fauna and flora as well as on the degree of specialization and the survival of species on it (Wallace, 1869; Simpson, 1952, 1953; MacArthur & Wilson, 1963, 1967; Mayr, 1965).

There are many instances of exotic plants and animals running wild and excluding endemic species in island floras and faunas. Another disadvantage for a localized population is that a predator

may turn its attention to the small population and cause catastrophic damage: for example, the fate of Stellar's Sea Cow (*Hydrodomalis gigas*), and Fur Seals (*Callorhinus* and *Arctocephalus*) or introduction of dogs, cats, goats, swine, cattle or rats onto oceanic islands.

Understanding the change from a "competitive" colonizing species to a "conservative" relict is at the heart of understanding rare species, and island biotas seem to lend themselves to the study.

2. *Some species are found in very small numbers widely dispersed in each community where they grow; they occur in many suitable areas over their geographic range.* At present, there appear to be no explanations adequate for the characteristics of this type of rare species. One doubts intuitively, for example, that a set of narrow niches exists widely spaced geographically and yet available for a particular suitably adapted species to occupy them.

The explanation may simply depend on combinations of chance factors. The occasional coincidence of several different, yet additive environmental factors may allow for the germination of seedlings of these "rare" species. It may be useful to see these coincidences in the same way that at sea many waves running at independent frequencies combine either to damp each other out or to reinforce each other into a giant wave. So in the case of some fish (*e.g.*, Herring, *Clupea harengus*), a coincidence of several favorable circumstances result in a successful spawning and survival of larvae (Hardy, 1959) which may affect the year-class composition of the population for many years (Hjort, 1914).

Among the advantages (or results) of a widely dispersed population is the fact that the population will probably be too dispersed to supply a favorable resource for pathogens, parasites, or predators. Any species which depends upon a rare species as a resource will have difficulty in finding its next prey (Janzen 1970, 1971, 1972).

Among the disadvantages of species having a dispersed distribution would be the possibility that if a new predator or parasite appears that consumes several different prey species without preference (that is, only in proportion to the numbers of each species present), the less frequent species will suffer disproportionate pressure. The Brown-headed Cowbird (*Molothrus ater*), whose large populations are maintained by parasitism on many species of songbirds, has been a major depressing factor on the population of rare

and localized Kirtland's Warblers (*Dendroica kirtlandi*) ever since the 1890s. At that time, extension of range made the cowbird numerous in the warbler's range (Mayfield, 1960). The expansion of range of the cowbird is not the direct cause, but the factor that allows us to follow the progress of this natural "experiment."

3. *Some species occur as a few individuals at scattered localities, or are restricted to a small geographic area or a single population.* In the extreme case such species are rare and endangered. One presumes that these species are the products of coincidence of a number of factors to which the population responded by accommodation. In the course of time the circumstances and habitat to which the population has been adjusted have changed. Thus on the Green and White Mountains of New Hampshire, Vermont, and Maine the habitat available to *Geum Peckii* or *Potentilla Robbinsiana* may have been more extensive during cold periods in the past or smaller during warmer periods.

The first and third categories of distribution are most vulnerable to events which may reduce their numbers or distributions to "Rare and Endangered" status. One presumes that plants such as *Franklinia*, *Ginkgo*, and *Metasequoia*, were reduced to a few stations before being found by humans, taken into cultivation, and thus being given a "new lease on life." They are now believed to be extinct in the wild. Similarly, capricious changes in the behavior of humans — expressed as dispersed recreation in the New England Mountains, have endangered the survival of Dwarf Mountain Cinquefoil (*Potentilla Robbinsiana*) at its relict site on Mount Washington. Another example of capricious human behavior (taking of plumes) also endangered the survival of Short-tailed Albatrosses (*Diomedea albatrus*) which once nested in good numbers on islets off Japan.

Is Rarity Correlated With Impoverishment?

During the decades 1930s through 1950s discussions of rarity were replete with references to genetic depletion to explain lack of aggressiveness. Aggressiveness implied wide ranges, large numbers, and conspicuousness. Following the work of Turesson (1925) and Clausen, Keck and Heisey (1940), reference to biotype depauperization was used to explain how "a species population" could lose the ability to occupy a variety of habitats. Although authors disagree on

the mechanisms involved, in general they agree that there was a reduction in genetic materials and hence adaptive potential in rare species.

Reflecting the then current ideas that rare species are either too young or too old, Stebbins (1942) distinguished two main types of rare plants: one type was once more common, widespread, and richer in biotypes (occupied more varied habitat); the other was never common, but diverged from a small group of individuals of a widespread ancestral species.

Three possible mechanisms leading to genetic depletion have been suggested: the founder principle, local selection, and inbreeding. Although the mechanisms are real, it is important for the purposes of this argument to realize that the studies which led to their clarification began with preoccupation with failure without establishing whether rare species are, indeed, less "successful." The Solbrigs (1979, Chapter 9) give a helpful précis of these ideas.

1. *The Founder Principle.* The founder principle is that a small emigrant population contains restricted genetic diversity. This hypothesis has replaced Wright's earlier one (1931, 1938, 1940), which was that depletion results from random genetic processes in small isolated populations. Wright called this genetic drift.

The founder principle is not appropriate as an explanation of the early stages of the sequence proposed by Ricklefs & Cox (1972), because the new colonists have the potential of aggressiveness and the old ones are the conservatives. In many other cases populations that have been reduced to a very few individuals have retained the diversity necessary to explode. The European ibex (*Capra ibex*) was reduced by hunting to one herd in the Italian Alps; the European starling (*Sturnus vulgaris*) was released as a small flock into Central Park in New York City. Both have shown great population vigor in increasing their populations and expanding their range, as have the many other species of plants and animals introduced to new continents and islands, most notably New Zealand (Elton, 1958). Native wild flowers of restricted alpine ranges in northwestern Canada, such as *Hedysarum alpinum*, became weeds along the Alcan Highway when it was first opened.

2. *Local Selection.* Some authors have suggested that genetic depletion is the result of a shift toward uniformity (homozygosity) in a constant environment. As an illustration, Krukenberg (1951),

studied a number of species found on serpentine rocks, where high magnesium content suppressed species characteristic of ordinary soils. The serpentine species grew well on non-serpentine soils when freed of competition. This suggests that variability in the genotype exists but is not expressed in the phenotype for a number of reasons, including masking by developmental processes or selection pressures leading to high mortality in the young stages. To the degree that genetic or phenotypic variability is restricted to the features which are suitable to the specific site, a small population on a homogeneous site can perhaps out-compete species whose local specializations are diluted by the production of less fit genotypes and phenotypes as a result of segregation of variable characteristics. Consequently, for such small populations variability is "good" only if we assume that the habitat will soon change. (O. Solbrig, pers. comm.).

If we postulate that the non-serpentine elements may be eliminated by their inability to tolerate high magnesium concentrations, this frees the serpentine species to become more homogeneously adapted to serpentine. For example, if a homozygote should arise which is superior or equal in fitness to the heterozygote in a constant environment, fixation of the allele would result. The homozygous population has the advantage in a predictable environment because each locus is self-sufficient and individuals can produce more viable young at low cost in mortality of ill-adapted gene combinations. The high cost is being less competitive in a variable environment. The heterogeneous population may be less fit in any one environment, but is able to live in a variety of environments by virtue of the diversity of its genotype. If there is a restriction in genetic resources, the mechanism of local selection to a specific adaptive background may be the most effective.

3. Inbreeding. Most field biologists now recognize that inbreeding has widespread importance while "random gene exchange" in a population is largely a theoretical abstraction.

Gene flow seems to refer to the movement of individuals from one population into another. Camin & Ehrlich's (1958) report on water-snakes (*Natrix sipedon*) on the islands in Lake Erie showed that despite strong selection toward non-banded forms, steady gene flow by banded immigrants onto the islands from the mainland prevented the completion of the selection process. In some cases

inbreeding and reduction in inherited variation is apparently of selective advantage.

In many plants even the extreme conditions of inbreeding, autogamy and asexual reproduction may be favored. In some species, inbreeding might be forced upon the population by events in the habitat such as scarcity of insect pollinators at the time of blooming as in the case of *Leavenworthia uniflora*, *L. exigua*, and *L. torulosa* (Rollins, 1963; Solbrig, 1972).

Once specialization for homogeneous habitat has started, the probability increases that isolated populations will lose gene exchange with their neighboring islands, and hence local selection pressures have an increased effect. Species on one or many islands should retain variability as long as they exist in many intercommunicating sub-populations; yet when the island's size is small or the habitat is uniform so that the whole island's population is one freely interbreeding unit, then homogeneity and specialization are favored. The major hazard may be that the area of the "island" and the number of islands among which a low level of exchange occurs become too low for the population to accommodate accidental events.

4. Masked Variability. One might ask whether in many cases there has been a depletion of the genetic resources at all. Until recently, many authors speculated on how genetic or biotype depauperization might be achieved, rather than measuring the degree to which variability exists. Recent studies of allozymes emphasize how much unexpressed potential variability exists. The term "allozyme" is used to designate different forms of an enzyme which are coded by different alleles at the same gene locus. The variation in form of the enzymes is examined electrophoretically. Extensive masked genetic variability has been found in fruit flies (*Drosophila*) (Ayala, et al., 1972a, b), in House Mice (*Mus domestica*) (Selander & Yang, 1969; Selander et al., 1969), and Horseshoe Crabs (*Limulus polyphemus*) (Selander, et al., 1970). Potential variability is not unexpected in such widespread and "successful" groups as the House Mouse or fruit flies, or in a species like the Horseshoe Crab which has outlasted so many others. Furthermore, Ayala et al. (1973) found large hidden potential of gene variability in isolated populations of the giant clam (*Tridacna maxima*) in the Marshall Islands, a species which they categorized as "an ecological analog of some unsuccessful evolutionary lineages."

It seems safe to conclude from this brief review that little direct evidence is available to support the idea that rare species hold any less genetic variability than common species.

Mayr has made three points which apply. First the characteristics of each individual or population are adaptive or not, according to their match with the specific habitat where the individual is found (Mayr, 1954). Secondly, genetic fitness cannot be separated from ecology because natural selection is an ecological process (Mayr, 1963). Thirdly, he distinguished two categories of rare species, one highly localized and the other highly specialized (Mayr, 1963). Thus he identified genetic and ecological mechanisms as operating in concert. This is a widespread attitude at present.

One should expect the genetic structure of a population to reflect the ecological (including mineralogical, physiographical, and geographical) problems to which the population is adjusted. One should consider the interplay of several historical events combined with suitable genetic adjustment by the population to be the forces which have produced those species which we acknowledge to be rare and endangered: i.e., have small populations on restricted habitats. Those extreme cases in which a species population is narrowly restricted to a few outcrops of limestone, gypsum or serpentine may be explained in terms of intense local selection on individuals on the specific habitat they occupy.

Stebbins (this symposium) argues that rarity is a result of close, highly specific, genetic adaptation to a demanding and restrictive habitat. Yet I know of no evidence that even these species have lessened genetic diversity. All this argues for the overwhelming influence of accidents and is the opposite of the classical concept that each rare species is a member of a coadapted complex which has special suitability in its natural community. This latter attitude has strongly influenced thinking about conservation in general and rare species in particular.

IF RARITY IS NOT FAILURE, WHAT IS SUCCESS?

Are size and numbers the best measure of biological success? Were the Mesozoic dinosaurs more successful than the Horseshoe Crab or the *Osmunda* ferns, which have apparently survived since the middle Paleozoic?

In the present section I will give several illustrations of cases in which outside forces are responsible for the establishment of pat-

terns of abundance. They suggest that a traditional assessment of success in terms of dominance and abundance may not be very helpful. They also suggest that a great variety of explanations may apply to the many "types" of distribution of species, rare and common, and that those explanations based simply on genetics or on competition may not be helpful.

In simplest terms distribution and abundance of an organism on the local scale depend 1) upon other organisms whose activities decrease the numbers of the species, 2) upon other organisms whose presence increases the numbers of the species, or 3) upon physical habitat. I will briefly illustrate the interactions with other organisms and then dwell at some length upon plant interactions with the physical habitat because of the peculiar relevance of these to the distribution and abundance of plants.

Predators and Parasites

Paine (1966) and Harper (1969) have pointed out the importance of herbivores in determining plant diversity. Grazers may remove dominant species which otherwise exclude inconspicuous forms and thereby increase diversity, as in the case of starfish (Paine, 1966) or sea urchins (Paine & Vadas, 1969). They may also suppress several species by their preferences as happened with sheep in the Welsh hills or in areas where the elimination of rabbits was followed temporarily by an unwonted species richness (Harper, 1969).

Harper (1977) said the liability of pure experimental stands to pests and diseases which have been considered nuisances may be the critical clue to the real factors regulating populations in nature. He used two vivid illustrations.

Prickly pear (*Opuntia stricta*) was introduced into Australia as a decorative plant, but it "escaped" from cultivation and became a noxious weed in large areas of native vegetation and sheep range. Introduction of a moth (*Cactoblastis cactorum*) which devours the cactus was followed by a population boom in the moth, then a rapid reduction in the population of Prickly pear and moth to a condition in which the moth population is kept small when long distances between clumps of Prickly pear increase the odds against a moth finding another cactus. The cactus population is controlled by increase in the moth population when moths can find more cacti. Without knowing this history it is unlikely that one would predict that a single insect would be that important or "fine-tuned."

Similarly, the introduced Klamath Weed (*Hypericum perforatum*) became an abundant and noxious weed on the range lands of the northwest U.S. and California. Introduction of the beetle (*Chrysolina quadrigemina*) led to a dramatic decrease in the population of Klamath Weed which now persists in shady places.

“It is believed that in the absence of previous knowledge of this programme, and unless he made specific studies, an entomologist or ecologist viewing the current picture would conclude that what we know to be the key insect species, *Chrysolina quadrigemina*, is not a significant influent of the stand of vegetation and that the few plants of Klamath weed seen here and there are not primarily limited by this insect. He might also erroneously conclude that this plant is a shade-loving species, since the beetle checks it much less effectively under shade, hence more survive there.” (Huffaker, 1964, *in* Harper, 1977.)

Janzen, in a number of articles, (1969, 1970, 1971, 1972) has shown that among tropical American leguminous trees, the numbers and distribution are strongly influenced by the probability of insect predators finding “the next” seed or pod, i.e., by the same sort of behavior patterns that result in a “stand-off” between *Opuntia* and *Cactoblastus*. This occurrence as isolated individuals, not as stands of single species, may explain why tropical trees depend upon insect pollination instead of wind pollination. Insect pollination gives greater long-range precision for pollination. (Janzen, 1967, 1968.)

These tropical trees (or natural selection) face a dilemma because they need both to attract some insects to act as pollinators and to avoid other insects which act as predators. The tropical trees will become overdispersed if the distance which allows them to avoid predation on their fruits makes it difficult for their pollinators to find them. Compensating mechanisms are, of course, producing masses of flowers, giving off strong odor, and surreptitious setting of fruits. As such, the adaptations illustrate the nice compromises which one suspects are characteristic of many of the actions of natural selection.

Biological Habitat

The size and distribution of populations are also regulated by the factors which govern the size and distribution of the species habitat. Only a small portion of these factors are directly dependent on natural selection. For example, the numbers of Great Tits (*Parus*

major) per hundred acres of mixed pine and hardwoods habitat depends in part upon the territory size of the Great Tits (Kluyver & Tinbergen, 1953; Krebs, 1971), and upon interactions with other titmice (*P. caeruleus*, *P. ater*, *P. palustris*) and Tree Sparrows (*Passer montanus*) (Krebs, 1971). These effects can be modified by changes in the behavior of Great Tits. The important factors governing the numbers of titmice, however, are the characteristics and geographic distribution of the mixed deciduous-coniferous forest (*Pinus sylvestris*, *Quercus robur*, *Fagus sylvatica*, *Betula alba*, *Acer platanoides*). The characteristics and distribution of the mixed pine-hardwoods forest are clearly not influenced by natural selection acting on titmice.

1. *Success and Succession.* The vegetation we see today is made up of changing combinations which reflect the particular responses of different species to gradients in habitat conditions (Whittaker, 1967), to the geographic distribution of its habitat, to its neighbors, and to events or accidents of the past which determine the geography of habitat and neighbors.

This leads to one of the most intractable of all the doctrines involved in the study of ecology. If one assumes, as many biologists have, that topography and vegetation "develop" toward stable conditions (mature landscapes and climax vegetation), one is drawn to the conclusion that it is a failing tactic for a species to "choose" ridgetops, marshes or beaches, i.e., habitats which are "immature" parts of the landscape. The vegetation of such places is called successional.

A number of ill-defined ideas have been associated with these "immature," or "successional" or "stressed" sites. In simplest terms, one can say they usually support fewer species and vegetation of lower stature than do other local sites which have deeper soils and more consistent water supply (Woodwell, 1970). Examination of this relation leads to the subject of "favorableness" (Terborgh, 1973) and to the characterizations that some theoreticians give to an optimal community: production, height, biomass, species-diversity, stability, soil depth, nutrient cycling, homeostasis, and populations characterized by "feedback control" (Odum, 1969; Margalef, 1968; Bormann et al, 1974). Successional sites usually experience wide extremes of temperature, and of water supply. They usually have soils low in nutrients and organic material.

May it not be that species on these sites must have "wide ecological tolerances" because the temperature, water supply and organic materials vary widely? If each species present occupies a "lot of ecological space" it will compete with other species over a wide range of "habitat parameters." If a new species appears, it is difficult for the newcomers and the established ones to adjust to coexistence by narrowing their requirements. Thus those species which persist exclude a number of others, and the "niche space" available for "species packing" is small. In areas where environmental characteristics vary less, each species can specialize without becoming vulnerable to the events which exceed the individuals' tolerances.

However, in simpler terms, it is as if some species are selected primarily by physical factors of their habitat (Wallacian selection) while others are selected primarily by biological factors reflecting competition from their neighbors (Darwinian selection). Two extreme types of "adaptive strategy" have been suggested: (1) to become a good competitor at the cost of being able to grow in "extreme" habitats; (2) to evolve the physiological apparatus needed to use the resources of an "extreme" habitat at the cost of being able to compete in biologically "favorable" habitats, i.e., the conditions vary less. Success in the first strategy might tend, if most of the regions' habitats are "favorable," to make the species widespread and abundant, while success in the other will tend to give the species a discontinuous distribution or, in the extreme case, widely separated populations.

There is an old biological adage (perhaps a superstition) that a limited amount of energy is available to an individual in the course of its life. Individuals use this energy in different ways, but only a certain amount of variability can be expressed in an interbreeding population. So the population must choose among alternative ways of life. Colonizing ability and growth rate tend to be inversely correlated with size at maturity and with longevity. Species can grow fast and reach sexual maturity at an early age, produce many young per brood, but if they do so, the individuals will be short-lived. The members of a species may put energy into growth and size before reaching sexual maturity, produce few young in which a large amount of effort is invested, and live a long time. Many papers have been written on this topic. Those by Cole (1954), MacArthur and Wilson (1967), Gadgil and Bossert (1970), and Gadgil and Solbrig (1972) present the main ideas. The symbols "r" and "K," although

[or because] tainted with association with group selection, have entered the jargon of ecology to represent these extreme "strategies." Of course, Redwoods (*Sequoia* and *Sequoiadendron*) and Douglas Fir (*Pseudotsuga Douglasii*) seeding in on mineral soil, growing fast in full sun (i.e., being early successional), and yet living to be ancient and huge trees are the "exceptions which 'prove' this rule."

2. *Physiographic processes as primary factors in vegetation.* If, as is consistent with current geomorphological ideas, one assumes that bedrock outcrops, sandy beaches, river bars, mountain tops or coves have been and will remain elements of the landscape indefinitely, then adaptation to any particular site along the spectrum of favorableness holds as good promise for survival as does adaptation to any other type of habitat. It is indeed the geographical distribution of habitat which has a maximum effect on distribution and abundance.

A number of botanists have pointed out the relation of plant distributions to forms of landscape (Kerner, 1863; Polunin, 1934-35; Raup, 1951; Sigafoos, 1952; Drury, 1956; Hack & Goodlett, 1960). Sigafoos (1952) considered frost action to be the major force determining patterns of vegetation in tundra, even on a microtopographic scale. Hack and Goodlett (1960) showed how the geology of the Little River region determined the major features of vegetation in a temperate forest region. Goodlett (1954) and Stout (1952) showed how microtopographic features and characteristics of the mineral soil determine the distribution of some trees in a deciduous forest.

This does not mean that there are not many important interactions among plants by which some species form an important part of other species' habitat. It does mean that the habitats of most plants are determined primarily by conditions and forces of the habitat beyond the control of the vegetation itself (as is the case with titmice and other woodland birds). These conclusions are to be contrasted with the conclusions of those who relate the structure and distribution of vegetation to forces contained within the vegetation; e.g. development of soil profile and resolution of interspecific competition.

One can recognize consistent parts of all landscapes: convex hill-tops, outcrops of bedrock, concave valley sides and depositional slopes grading into the bottoms of the valley and floodplain. Along

the coasts one recognizes salt marshes and sand dunes. Each of the landscape units tends to have a characteristic community of plants, although in some areas one landscape unit may have several recognizable associations of plants and in other areas one association occupies several landscape units. It may be that a coincidence of numbers of species of plants with the number of units of topography in temperate regions is responsible for the existence there of many botanists who are convinced of the integrity of plant associations. In arctic regions (where the number of species of plants is too few) and in tropical regions (where the number of species is too many) students of vegetation have characteristically been less sanguine about the consistency of units of vegetation.

Vegetation which occupies valley bottoms will tend to have a continuous distribution. Vegetation which occupies sand dunes, sheltered coves at stream headwaters, or hilltops tends to occur in discontinuous clumps.

In classical ecological theory the floras of mountain tops were considered both relicts of formerly widespread floras (Pleistocene) and occupants of habitats destined to be destroyed by erosion, the process of peneplanation. Hence the relict species were readily considered doomed to extinction. It is perhaps poetic justice that other species persist on "islands" at the opposite end of the habitat spectrum, the shaded, well-watered coves with deep soils under isolated patches or islands of "post climax" vegetation. These coves are actually as much islands as are the knobs of the mountains and they often harbor rare species.

If species follow a river, the distribution and "tactics" of dispersal should be different from those of a species which lives on ridges. The measures of successful dispersal are as different as the measures of stature are different between the hardwood trees of the deciduous forests and the spring wildflowers which grow on the floors of the deciduous forests in larger numbers than the trees.

Plants which grow in ranks usually use the wind to disperse their pollen. To use the wind, the plants must also occupy the "canopy," hence the technique is associated with "dominants." The use of the wind suggests that outbreeding may be either of special importance or simply a coincidence, because these plants often differ markedly in their dispersal mechanisms. Their dispersal mechanisms are suited to where the plants "want" to get to.

First, trees such as Oaks (*Quercus*), Beech (*Fagus*), or Chestnut

(*Castanea*) which grow along water courses have a "continuous" geographic distribution and their seeds are dispersed at short range. They drop or may be carried short distances by animals. The difference in purpose also results in a difference in "tactics" with regard to supply of nutrient for the seedling. Trees which have continuous distribution may emphasize a subsidy for the young plant to maintain it while it becomes established.

Secondly, some trees face the problem of dispersing their seed between islands. Aspens (*Populus tremuloides*) live on sand plains, ridges or on the coarse material collected at the end of solifluction lobes. They have seeds carried by the wind. The seeds need to be light, and if the seed lands on disturbed soil it is not likely to be suppressed. It can start to photosynthesize at once.

Some authors have argued that highly effective dispersal mechanisms are adaptations by which species of fugitive habitats reach another habitat before their successional stage is replaced. Put another way, these dispersal mechanisms are adaptations of last resort by which a species is able to escape extinction. In contrast it may be that these characteristics which we now associate with "r" are really adaptations by which species occupying islands of habitat may get to the next island. The seedlings germinate in little pockets of moisture, in drifting sand or between rocks and grow rapidly in the full sun. The effectiveness of dispersal is illustrated by the appearance of Aspens on treeless Seal Island, Penobscot Bay, Maine, in 1979, sprouting after a fire set by lobstermen in 1978. Seal Island is seven miles from the small forested islands of Matinicus and Ragged and nine to ten from Isle au Haut and Vinalhaven.

Thirdly, using Burdock (*Arctium*), Beggar-ticks (*Bidens*), Forget-me-not (*Myosotis*), or the awns on many grasses as illustrations, if the seed sticks to the fur of animals, one presumes the plant can grow well along animal trails, or where they rest.

The evidence that some animals and plants reduce their adaptations for dispersal when the distances between suitable sites (on islands) exceed a certain amount, argues that the dispersal mechanisms are effective at present and only in part reflective of events of the past.

Adaptations suitable to river banks, ridge tops, or sand plains have "preadapted" plants of "stressed" sites to occupy other sites which have been deforested. Under these circumstances such species can expand their range, as have some wildflowers in occupying the

road verges along new highways in the north (e.g., *Hedysarum alpinum*, *Epilobium angustifolium*, or *Linaria canadense*), and thus shift into a habitat where they suddenly become a pest. In this way it may be “easy” for a usually rare plant species to become abundant. For example, Mayflower (*Epigaea repens*), which was listed by the New England Wildflower Preservation Society as a rare plant not to be picked, becomes an abundant weed after a fire in the oak-pine woods of southern New England.

The major patterns of plant distribution are determined by rainfall and temperatures, then by physiographic forces acting on a time scale far exceeding the life spans of the longest lived trees. These control regional abundance by defining the total area of habitat. In the case that we define success as survival of genes through geological time, it may be a preferable strategy to occupy beaches or ridges where mineral soil is exposed because geological processes guarantee their perennial presence. It should then be “prudent” to avoid the temptation of growth to size and dominance, hence dependence on high levels of nutrients and high moisture supply in the soil, because relatively minor geological events can change a “mesophytic” site to an “early successional” one.

WHAT CHARACTERISTICS ALLOW SPECIES TO SURVIVE?

During the past decades people who have worked with insects and birds have contributed extensively to knowledge of populations, their regulation, and hence to theory of pest control and doctrine of conservation. To a large degree problems of pest control have been addressed by entomologists and problems of conservation have been the concern of ornithologists. During these years it was difficult to get many zoologists (or botanists) to consider seriously that plants are alive and subject to natural selection.

Birds and insects are active and mobile. They have a fixed life span through which they “rush”; if they have not reproduced successfully in that short life span they have no “fitness.” The press of this commitment has dominated a lot of thinking about dangers to populations. Among these hazards was the “random walk”, the idea that population fluctuations might get larger and larger until the population went extinct. During the years of debate between proponents of “density dependent” and “density independent” regulation, it was widely argued that unless a species had characteristics by

which its populations were regulated, it would face inevitable, rapid extinction.

Advantages of Discrete Subpopulations

Andrewartha and Birch (1954) suggested that movements among population centers are active elements in population biology, without arguing specifically that such movements make "the random walk" irrelevant. MacArthur and Wilson (1963) used similar ideas as the foundation for their "theory of island biogeography", again without emphasizing the implications as to the regulation of populations. Nisbet and I (1972) argued for what we called the *Daphnia* model — that the chief defense a widely distributed population has against extinction is the movement of individuals between population centers. Such movements ensure the re-establishment of local centers because it is highly improbable that any single catastrophe will affect more than a part of the species range at any one time.

Movements among, and differences in survival and reproductive success in preferred and non-preferred habitats have been found to be important parts of the population biology of successful, widespread and outbreeding species, such as Herring Gulls (*Larus argentatus*) (Drury & Nisbet, 1972) and Great Tits (*Parus major*) (Kluyver, 1951). A mobile population of individuals excluded from breeding in preferred habitats exists in both these species and in many songbirds (Hensley & Cope, 1951; Stewart & Aldrich, 1951). In many animal species there is a small percentage of persistent "wanderers." Many animals are subject to periodic eruptions as a result of "uncontrolled" growth in several sub-populations. Such eruptions disperse the population and, even though accompanied by massive mortality, may allow some individuals to survive and become established in unoccupied habitat. This was apparently the case with the colonization by Evening Grosbeaks (*Hesperiphona vespertina*) of eastern North America in the late 1930s.

An illustration of ecological advantage in a population's being divided into sub-populations is given in the history of the Laughing Gull (*Larus atricilla*) in New England since 1875. Between 1875 and 1900 there were fewer than 50 Laughing Gulls in Massachusetts (MacKay, 1893) and about 35 Laughing Gulls in Maine (Norton, 1924). In Massachusetts, Laughing Gulls all settled on one large island, Muskeget, where by 1940 there were about 20,000 pairs (Noble & Wurm, 1943). Meanwhile the Maine population had been

disturbed by man and sheep and had moved about between seven islands; it grew to about 250 pairs by 1940 (Palmer, 1949). After 1940, the Laughing Gull population of both states decreased. In Massachusetts, where all the birds occupied one island and its surrounding waters, the population had fallen to about 250 pairs in 1972, but the Maine population, still divided into five colonies each with somewhat different surrounding waters, remained at 250 pairs, i.e., equal to, instead of one percent of, the Massachusetts population. The population increased again in Massachusetts during the 1970s when the birds moved to a new gullery on Monomoy Point, Cape Cod. Similarly, the Heath Hen (*Tympanuchus cupido*) got into trouble after being isolated in a single population in a single habitat on Martha's Vineyard, Massachusetts (Gross, 1928).

The effects of population exchange between habitat centers are significant in management policy for rare species, and will be discussed below.

Adaptive Advantages of Plants

Plants and many animals apparently differ in the degree to which problems of rarity and isolation of sub-populations become serious. Most plant species (other than community dominants) probably exist in more or less isolated stations with little gene flow between them. Even many insect-pollinated species have only 10–20% cross-pollination and are mainly self-compatible. This allows a local population to build up its numbers in the habitat to which it is adjusted (the strategy of inbreeding or asexual reproduction), but yet continue to produce a low percentage of more highly diverse young to “seek” another habitat or to adjust to changes in the local one (the strategy of outbreeding or sexual reproduction). An additional pool of masked variability among plants may be provided by polyploidy.

Many invertebrate species resemble plants in having resistant resting stages, and some invertebrates have the adaptation of being able to alternate between sexual or asexual reproduction (and having the potential of self-fertilization among hermaphroditic molluscs). Another element of this adaptive complex of sessile animals and plants is to develop adaptations to ensure wide dispersal of diaspores, e.g. by ocean currents in marine invertebrates, or by the wind in spore bearing land plants.

Harper made the important point that among many plants, reference to asexual reproduction is not helpful because production of “ramets” is a way of producing more of the same individual — not

producing a new genetic individual. Harper (1977) defines a "ramet" as an additional morphological expression of an existing genetic combination and a "genet" as a genetically determined new individual. The problem of separating an additional individual from modified branches of an existing individual may be serious in quantitative studies of plant populations, but the ability of plants and many invertebrate animals to "choose" between these systems of spread is of great importance as "strategy." Many ideas in the following discussion were stimulated or brought into focus by reading Harper's splendid book.

1. Once a seedling is established, its growth implies that its genetic combination is suitable for the site. It is therefore evident that the individual should duplicate that gene combination rather than risking waste of genes by producing different and statistically less likely-to-be-suitable combinations. Many species of plants have extensive systems of branching stems, rhizomes, sprouting roots, runners, tillers, etc. by which the individual builds up "its numbers" to occupy a space to which it is suitably adapted. According to this strategy "genets" are new combinations of genes which are dispersed "seeking" other suitable habitats. The dispersed individuals risk astronomically high rates of mortality in the "hope" of finding a new site where (it is reasonable to assume) a slightly different gene combination is likely to be suitable. Trembling Aspens, Beech (*Fagus grandifolia*), and American Chestnut (*Castanea dentata*) are examples of forest trees which form clones. The underground stems and sprouting roots of sedges and grasses which form the sedge mats of bogs or the turf of meadows illustrate the importance of this ramet system. Corals have a similar system of budding "branches."

Some branching stems grow underground and while they proliferate and grow forward, they are dying behind. Thus for an individual of Cinnamon Fern (*Osmunda cinnamomea*) growth and branching may lead to essential immortality as well as to production of a large number of virtually exact copies. For some plants and some animals successful establishment of a single individual will have tremendous implications, in contrast to the situation among most animals, especially birds.

2. In general plants and animals are fundamentally different in their opportunity to "extemporize" on the development of an individual and its parts. Plant parts have great latitude of development. Single lower branches of open-grown trees may be larger than entire

other individuals while the lower branches of trees grown together may be short, suppressed, and soon die. A tree may have a straight bole up to the level of the canopy and there open out into a "bush," or that bushy growth form may start at the ground. Trees growing in exposed places, on ridge tops, edges of fields, or after fires may have some branches whose individual histories are as different from the rest of the same "tree" as are different clumps of *Osmunda*. Observations of the forms of trees (Horn, 1971) and review of the processes of plant embryology and morphogenesis (Torrey, 1967; Steeves & Sussex, 1972) suggest a great deal of independence for the several meristems and different elements of a plant body. While a plant continues the tremendous potential for differentiation in its initials, an animal is generally committed to rigid form at the unfolding of the early cell divisions of the embryo. It may be fair to say that an individual tree shows less unity of integration than many ecologists have credited to whole plant communities.

3. One of the special aspects of plant biology is the observation of "delayed maturity": many plants seem to be unhurried about their production of offspring. This contrasts with a model prepared by Cole (1954) which has affected a lot of thought about animal populations and reproduction. That model, in part, shows that an organism which reproduced in its first year, produces two offspring and dies, will be represented by as many offspring as an individual which waits until its second year and produces one young every year forever. In many cases plants do not seem bound by this compulsion to reproduce. For example, a dune grass (*Ammophila arenaria breviligulata*) will grow and produce ramets for many years, then suddenly burst into flower when its roots are exposed by a blow-out. At the same time a tree being overwhelmed by the movements of the dune will produce a heavy crop of flowers and seeds. If a plant occupies a site, it is of little benefit to it to produce seeds which germinate under itself and are shaded and suppressed each year. But once the individual is exposed to conditions that indicate its imminent demise, it is stimulated to produce an abundance of offspring. It is as if the benefits of reproduction by genets are not consistently worth even the minor costs as long as an established individual occupies the site with some sort of "de facto" immortality by ramets.

In other cases there are plants which grow for a number of years and flower, then die. If the flowers are picked off, the plant returns

to vegetative growth, continuing to live. This pattern of behavior is incomprehensible to an ornithologist, most of whose theory is based upon preoccupation with a rush to sex and to inevitable early death.

4. Plants, like some invertebrate animals, produce elements which can persist in the soil for years, the "seed bank," of Harper and White (1974), until they receive clues that conditions have become favorable. Thus, a set of genes can "wait" for suitable conditions as well as be carried to places where the set may become established.

An additional characteristic by which plants differ from active vertebrates is in their ability to exist suppressed (sapling under the canopy or an herbaceous plant in the midst of grass turf) until release. Without thinking, we suggest that once started, life of an individual proceeds through stages of a small embryo, growing-youth, producing maturity, and declining powers of old age. Russians (e.g., Uranov et al, 1970; Uranov & Smirnova, 1969) have suggested that plants have life states which can be "recycled." A plant which has been suppressed for many years and has exhibited the characteristics of "senility," may be released and quickly take on the vigorous growth and activity of a seedling. A parallel can be formed in the lives of individual branches or other ramets. These reflect very different systems of embryology than we normally conceive of, having learned primarily animal embryology.

5. Structural diversity is characteristic of plants and is a "mechanism" by which plants make phenotypic adjustment to the place where they find themselves, because they are unable to move. This structural diversity may make difficult the recognition of species in many plants. In contrast, many active animals tend, because of the constraints of their activity, to be uniform structurally. An extreme case is found among some plants of the north, such as Grey Willow (*Salix glauca*). This plant varies in leaf form from small, spatulate, acute tipped forms in mountain stream beds in Alaska to large orbicular leaves in eastern Canada (Figure 1). One presumes that this variability parallels and reflects a physiological variability adjusted to features of the habitat in which the species grows in its North American range. It also occurs across Siberia and northern Europe.

Earlier, I suggested that an important reason for there being few

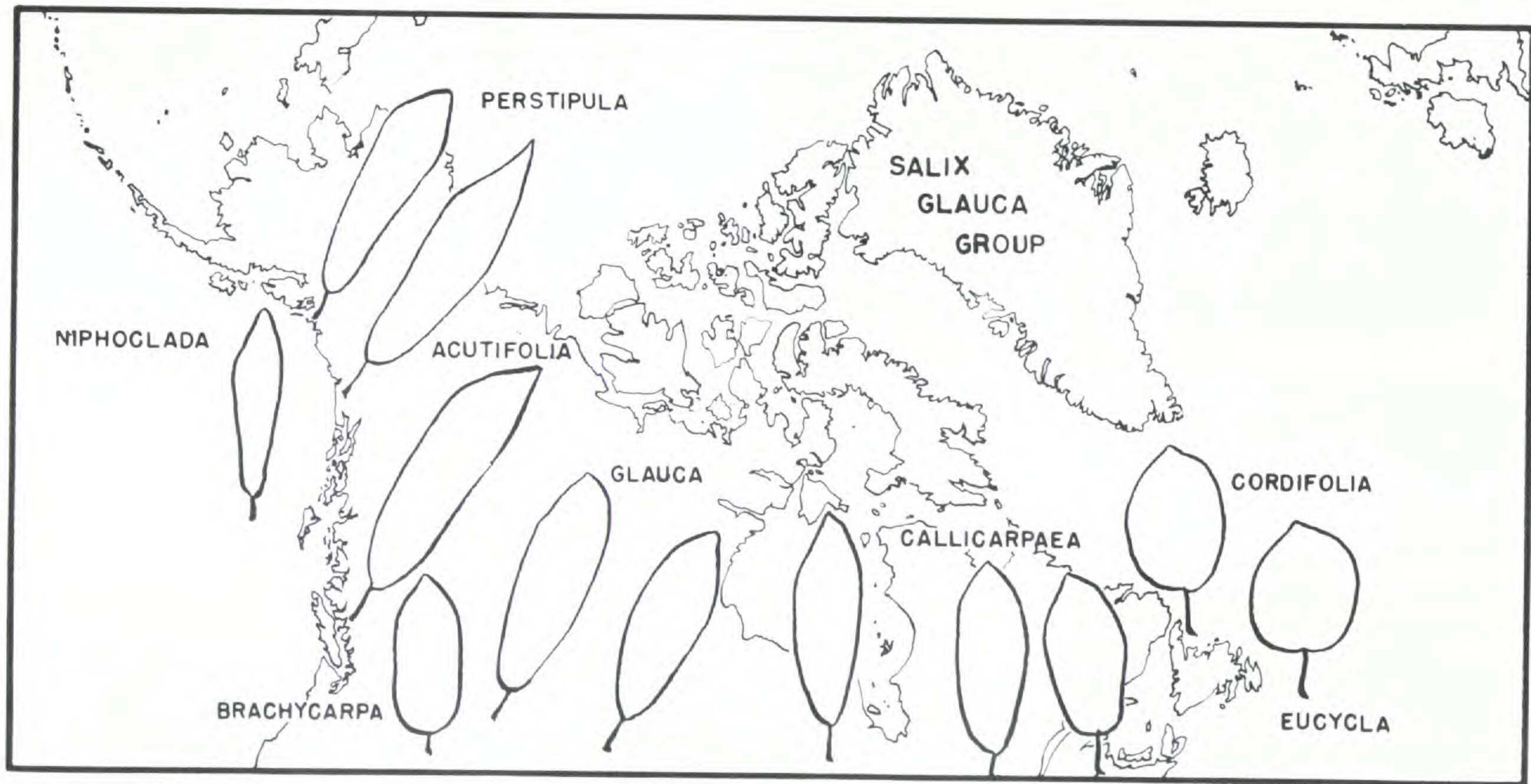


Figure 1.

Distribution of leaf shapes of Gray Willow across North America

The extreme variation in shapes of leaves suggests that the species contains a wide range of ecotypes. Trembling Aspen occupies similarly diverse habitats without evident morphological variation. One wonders either how the genetic structure of the species retains this wide variability or why other species do not express as much variability in form as does Gray Willow.

species in habitats whose environmental parameters vary widely (soil moisture, temperature) and whose landscapes are uniform, is that in order to survive species must have wide ecological amplitudes. Large differences in rainfall, temperature, soils, and other habitat features are found across North America and Siberia in the range of *Salix glauca*. One should not be surprised to find similarly large variability in the structural expressions of species having "wide ecological amplitude."

But this challenge of the environment presents a dilemma to the long term adaptive mechanisms of the species. To what degree can a "species" go on accreting additional variation without straining the equilibria which are suggested to exist in "adaptive gene complexes" (Mayr, 1963)? *Salix glauca* may be an extreme in the ability to tolerate variability. What is the case in those species groups (e.g., *Astragalus*, or many grasses, *Calamagrostis*) in which the "strategy" seems to be to divide up into many small populations which seem to have partial reproductive isolation? Their reproductive isolation is often based more on geography than on biological barriers to interbreeding. Again it is suggestive that the greater ability of plants to tolerate structural differences may allow production of many individuals which appear to be or are indeed "hybrids", most of which are "weeded" out by continuous natural selection.

In many cases, the numbers of these forms do not increase because counter selection can keep up with and prevent extensive "introgression." Work on *Drosophila* (Thoday & Boam, 1959) suggested that even among animals extreme variants within a single interbreeding population may assort preferentially so as to retain the extreme forms. Among plants the not infrequent coexistence of recognizable "varieties" within one species in one geographic region (dependent on habitat differences) suggests the everyday importance of selection of individual gene combinations by their habitat.

In other cases hybridization is associated with polyploidy, and hybridization together with high levels of polyploidy seem to lead to apomixis (the production of seeds without fertilization) (C. Greene, pers. comm.). Apomixis provides an extreme case of adaptation to inbreeding and may be a "solution" that plants have "found" for the problem of controlling variability. Apomixis can be seen as a mechanism which provides for better setting of seed especially in cases in which high levels of polyploidy present problems to proper pairing of chromosomes at meiosis. At the same time the high levels of

polyploidy provide masked variability and partial meiosis can supply opportunities for recombination of genes.

Apomict species present an especially awkward problem to biological systematists because it is not clear where species lines should be drawn either by morphological or behavioral characteristics. They seem to provide a case in which the now classical biological species concept is not helpful.

One wonders to what degree some problems in drawing species lines represent real difficulties reflecting the "tactics" of plant species, in response to special habitat interactions. The lines drawn, of course, also reflect the personalities and experiences of the botanists who have worked on them (splitters or lumpers). The clarification of such difficulties may be important when required in establishing the validity of species groups which have been suggested for critical or other special legal status. For example, a species of *Calamagrostis* has been suggested for inclusion in the critical areas study in Maine. Louie-Marie (1944) made the following suggestive comment about it:

"Calamagrostis Fernaldii Louis-Marie

The plant is certainly baffling. Following Kearney's identification, Fernald puts this collection in *C. perplexa*, but always admitting it as not identical. Scribner has assimilated it with *C. Porteri*, undoubtedly as a "pis aller," and before the publication of *C. nemoralis* Kearney. About this plant Wiegand and Eames took a very different position. In their Flora of the Cayuga Lake Basin, they wrote, under *C. perplexa*: "an inspection of that plant shows it to be not the same, and more like an offshoot of *C. Pickeringii*. The Danby plant is related to *C. Porteri*." In general habit the Piscataquis County plant looks like *C. Pickeringii*, var. *debilis*, but inside its spikelets there is the abundance of hairs that characterizes *C. perplexa*. Nevertheless, it cannot be united to the Danby type, which has "scattered culms" and "two tufts of hairs at the base of the leaf"; it is caespitose and has no tufts of hairs at the summit of its sheaths".

Though a subject with a long history and one of debate between Darwin and Wallace, geneticists have perhaps prudently avoided facing the problem: "when and why (the selective advantage, not the mechanisms) do two populations 'become' two biological species?" Are chance events occurring in geographically isolated populations sufficient conditions as well as necessary conditions?

WHAT SHOULD BE DONE?

Actions to be considered in a program of rehabilitation of a species should include assessment of biological and human values: the human values being those values perceived by people, and the action being applied within the biological contexts of each species. Each critical species needs to be understood as itself.

Species which are closely adapted to a narrow habitat which has a patchy distribution as if on islands are of course especially vulnerable. Thus, the problems of dispersal and conservatism that have traditionally been associated with island faunas and floras deserve special consideration. A number of published articles exist on this general topic, because theorists interested in the mathematical theory of "Island Biogeography" have developed the theme. According to theory, and contradictory to traditional conservation practice, even a patch of wilderness climax ecosystem will suffer attrition of species. Species with a rapid turnover of the population or species which require large ranges are especially prone to this attrition. On the other hand some species seem to do very well on small islands. Rare species of plants found by Rand and Redfield (1894) more than eighty-five years ago on Mount Desert Island have recently been found at the same stations.

Because most species of concern already have been reduced and to some degree isolated, their habitat can be assumed to be coveted by other (especially human) uses. This raises one of the most pressing human problems: "At what level is the species important?" One can predict that in the future decisions resolving competing demands will not be justified in absolutes, although the rhetoric of the proponents may seem to demand it.

Plants have some special attributes which need consideration; for example, "old growth" forest has a special importance that senile animals lack. Many humans value a shabby growth of old-field pine, although foresters and lumbermen are impatient with them. Many dedicated conservationists enjoy rolling vistas of meadows and prefer them to the "wall to wall" trees which often result if we "let nature take her course." While much of the charm of animals is seeing them undisturbed against a suitable landscape, the topographic element is in many cases not critical for the animal species. In contrast, as I have said, I believe that plants have a geomorphic basis for their distributions and suggest therefore that actions to be

taken must consider a geomorphic context for plants. Thus, one needs to consider size of areas and sorts of landscape, as well as connection among areas to be preserved.

Some species have special human appeal. Thus, we can say that some species are peculiarly useful as tools to be used in operating within existing social institutions to create or restore circumstances that will be pleasing to us. Our work as activists is directed toward goals which combine a sense of responsibility toward the organisms around us and the conditions which make humans feel some contentment. I will discuss this further in Section 5.

Steps to be Taken

The arguments in this paper suggest a number of courses of action in the interests of any given rare and endangered species.

1. Most important of all is to guarantee that several adequately large areas of suitable habitat exist. The size of the area and the patterns will depend on the peculiarities of the species.

2. It seems prudent, as the first step in rehabilitating a relict population, to take active steps to encourage it to break up into a number of more or less independent sub-populations. This, of course, is exactly contrary to traditional protectionist policy.

The existence in most populations of a low rate of outbreeding between independently maintained sub-populations emphasizes the importance of local populations of a wide-ranging species now isolated by changes in habitat. The bald eagle (*Haliaeetus leucocephalus*) is broken up into several population sections, most conspicuously those on the Alaska coast, the Great lakes, Maine Maritimes, and Florida. Each of these sub-populations (whether recognized by taxonomy or not) should be regarded as a population of major importance in the survival of the species. Interchange among populations should be encouraged.

3. It is unlikely that all young produced by any species naturally in the wild are necessary to maintain the local population. In fact, Kluyver's (1966) study of Great Tits in a closed population on the Island of Vlieland showed that adult mortality was reduced by artificially decreasing the number of young. Furthermore, although the details of behavior differ from species to species, it seems clear that many young are excluded from breeding by social interactions with established territory holders (e.g., Kluyver & Tinbergen, 1953; Wat-

son, 1967; Krebs, 1971; Carrick, 1972). This is of course obvious for seeds which fall under their parent plants. Therefore in taking action on behalf of a relict population it seems reasonable first to measure the recruitment necessary to maintain adult breeding population size and use any reproductive surplus to establish new colonists in vacant traditional habitat. In fact, it seems probable that releasing young on former habitat now empty could improve the chances of survival of the young to the degree that their survival in the traditional habitat is compromised by competition from their parents and other established adults (Kluyver, 1966).

4. The evidence just reviewed referring to the genetic and geographical structure of wild populations suggests that problems of restricted genetic variability resulting from taking small samples from the wild into captivity will not necessarily be serious. Present understanding indicates that the danger of the founder principle (genetic homogeneity resulting from beginning with a small number) or inbreeding will not inescapably be disastrous and that many dangers can be overcome. The samples taken from wild inbred populations may already be homozygous (e.g., *Leavenworthia*, Solbrig, 1972), or they may not be (*Avena*, Jain & Marshall, 1967; *Tridacna*, Ayala *et al.*, 1973). What happens to them in a breeding program is what matters and enough is known of population genetics now to develop a promising strategy for successful breeding.

5. The traditional purpose of a breeding program is to release a large number of potential recruits to the wild population. An additional major purpose should be to increase variability in the population and allow natural selection to select suitable phenotypes from among those individuals released.

Any breeding program should follow a strategy tailored to the peculiar characteristic of each species involved, plant or animal. One major danger would be to continue inbreeding in captivity over any significantly long time. Inbreeding is usually encouraged consciously or unconsciously in a breeding program and may further reduce variability.

Another danger is the effects of unconscious selection for characteristics suitable for cultivation or captivity. In the real world natural selection acts against certain sets of characteristics and for other sets. In captivity selection by the breeder almost undoubtedly does the same (i.e., for "handsome birds" or "tame" ones, or simply those that will survive and breed in the greenhouse or cage). Conscious or

unconscious selection by breeders seems a reasonable explanation of the declining fertility and vigor in populations of Ne-ne Geese (*Branta sandvicensis*) and Aleutian Canada Geese (*Branta canadensis leucopareia*) kept in captivity.

These arguments suggest that variability should be deliberately promoted in breeding stock. It is generally agreed that the promotion of variability is the function of sexuality and this variability, *inter alia*, increases the probability that some percentage of offspring will become established on habitat away from the breeding site. The cost is a high mortality rate (often over 90%) in nearly all wild populations studied. The desired variability can be promoted by ensuring constant turnover in the breeding stock, by introducing new breeders continuously from the wild, and by releasing as many offspring after as few generations of captive breeding as possible.

6. Conservationists have been quick to criticize lack of success in a program of captive-breeding and release. One often hears about the very high mortality of game-farm pheasants. Granted that such birds had no chance to learn how to survive on their own, it is important to have reliable measurements of mortality and compare these to data on a per-egg-laid basis for a wild population. Even in a successful, increasing species such as a Herring Gull (*Larus argentatus*), mortality rate is extremely high. For example, a pair of mature gulls can expect to live 10–12 years and produce 30–36 eggs. Even if all but three of these die before reaching reproductive age, the population is increasing. Mortality among seedlings of a Sugar Maple (*Acer saccharum*) or larvae of a Salmon (*Salmo*) is almost incomprehensible.

Because of the high mortality that must be expected, large numbers of young should be continuously produced and released over many years in a reseeded trial. No young at all may survive for several years then suddenly a successful year-class appears. Because of the variability that will be needed for the first stages of population rehabilitation, especially large numbers should be produced. This is also especially important in dealing with conservative species, those which avoid colonizing unoccupied areas. Each species, however, is likely to have its own peculiarities. Present evidence indicates that releases of wild-caught turkey poults have succeeded where releases of captive-raised ones have failed for years in New England.

It should be easier to reestablish plants as compared to animals,

because of the greater ease of growing plants under cultivation and the greater control over individuals in transplanting to suitable habitat. Seed is available from wild plants and one does not have the impression that all the seed is needed to maintain the wild population. Lavish numbers of offspring can be raised and transplants repeated until some individuals become established. There seems to be less intuitive concern at expending young ones we have raised, and it should be easier to overcome the idea that if transplants fail the effort has been poorly conceived. We may still have to overcome the traditional attitude that humans should not intrude on the ways of nature, but those interested in plants seem to have more practical or less emotional attitudes than do animal lovers. After all, they weed their gardens.

If one has the faith that biological problems can be solved by the application of imagination, effort, and resources, one must believe that the breeding can be done. The risks may be high, but cross-breeding and releases have more promise of success than does the alternative. The practice of jealously guarding those young that are produced "naturally" may be as damaging a tactic as can be used, reminiscent of the biblical character who jealously hoarded his single talent.

PARADIGMS, POLICIES AND POLITICS

Clearly the experience of students and the philosophies or models to which they were "imprinted" affect the conclusions drawn and generalizations made as much as does the biology of the organisms studied. These influences need to be sorted out in the search toward understanding the biology of rare species and proposing steps to be taken to ensure their survival. Natural Selection is a sweeping generalization and one of the most powerful intellectual tools developed by any philosophy. But once one acknowledges that natural selection acts on individuals, each in unique situations, one is faced with a redundancy of detail that challenges generalization. As each individual plant or animal must solve its own problems in its specific habitat, so those people who assume responsibility for preservation of landscapes, habitats, and species must address situations that include a wealth of details, for which few generalizations are helpful.

In this section I will review some philosophical attitudes and present arguments familiar to many ecologists. This may seem gra-

tuitous and roundabout to those by whom it is already acknowledged. But because this paper will be read by conservationists whose commitment is emotional, not scientific, and because most of the rhetoric of contemporary environmentalists includes arguments which I believe are false, I will repeat the argument.

During the last three decades we have witnessed chronic confrontation between proponents of industry and of environmentalism. It is usually believed that this confrontation is one between fundamentally different assumptions, but I suggest that the two are using the same "paradigm". The two major forces, both the ecological imperative (which has as its ideal the wilderness climax) and the market place imperative (which has its ideal in free operation of supply and demand) believe in what I believe would constitute a miracle. The miracle would be that the sum of individually selfish acts would create a system which is beneficial to all. The basic selfishness of human nature is well-known. Its "naturalness" was a foundation of 18th century thought. Selfishness of actions and motivations are also the basis of Darwinian natural selection. . . . Whence, we should ask, comes the delusion that individuals were supplied according to their needs in the "state of nature" or that the market place cares for the needs of the poor?

The paradigms are deterministic, and the people who use them are oblivious to their implications. I think that individuals' "needs" and "the poor" are irrelevant to these models. In the deterministic model it is assumed that conflicting forces interact within the system until an equilibrium is reached. The equilibrium is then maintained by a balance of forces. Balance plays a central role in the arguments both of the environmentalist and of the market economist. If our world were indeed to attain equilibrium, it would be a dull place.

The ecological imperative is based on early 20th century ecological models which used the "theory" of succession to argue that with passage of time communities achieve a particular, preferred configuration of species, and are characterized by a variety of "good things": maximum productivity, diversity, efficiency, large biomass, nutrient cycling, stability, "information content," etc. These are the climaxes. Disturbance of a climax was damage, which, it was believed, set into motion forces which led to "recovery." In the same model it was believed that reduction or excess of populations initiated compensatory mechanism and led to reestablishment of equilibria. It has been asserted that before the advent of western

man natural populations were saturated and stable at the carrying capacity of the environment.

Repeatedly, these days, one hears conservationists using the dogma that each species fills a function in a holistically organized community whose sum creates a circumstance which guarantees the needs of all component parts. If one pulls at one part, one affects all other parts. If we do not know what the function of a part is, we should not tamper for fear that we may 'do irreparable damage.

I will not go into my contrary arguments here because they are published elsewhere (Drury and Nisbet, 1971, 1972, 1973). My arguments are based on observations of lack of stability of numbers, lack of coupling among subsystems, redundancy of systems, and opportunistic use of several systems by many elements of what we might like to call one ecosystem. Experience indicates that one can seldom prepare a model which will allow a *a priori* predictions of the effects of manipulation of parts of a natural system. What effects will be caused by removal of a conspicuous species such as American Chestnut (*Castanea dentata*) from the Appalachian forests or of Herring Gulls from the New England shore in the late 19th and early 20th centuries?

During the last twenty years of renewed study of natural selection, most students have come to doubt (as did Darwin) that natural selection can select one species for the benefit of another species. Harper (1977) has cogently put it:

"A theory of natural selection that is based on the fitness of individuals leaves little room for the evolution of populations or species toward some optimum, such as better use of environmental resources, higher productivity per acre of land, more stable ecosystems, or even for the view that plants in some way become more efficient than their ancestors. Instead, both the study of evolutionary processes and of the natural behaviour of populations suggest that the principles of "beggar my neighbor" and "I'm all right Jack" dominate all and every aspect of evolution. . . Natural selection is about individuals and it would be surprising if the behaviour that favoured one individual against another was also the behaviour that maximized the performance of the population as a whole".

Harper's comments express the doubts about the achievement of compromise when resources are limited. In the same way that many conservationists plead: "let nature take her course;" so the free

market proponents say: "let the market act." The patchwork of what industrial spokesmen patronizingly call "government intervention" speaks of the reservations that our society feels about a competitive market system's actually working for "the public good," when different elements of society have different goals. The exploits of John D. Rockefeller, Andrew Carnegie, *et al.* should convince doubters.

Another expression of the expectation that natural systems lead to a utopia is found in the ideal that native people have developed "proper" conservation ethics. If all animals are in balance, then true natives are in balance. We close our eyes to the forces of starvation, brutality and disease which kept "native" populations low whenever they pressed on their resources. Let us consider the people of the north. We should expect their ethics to be suitable to their environment and to their strategies as predators.

In recent history the Eskimos were a people dominated by the capriciousness of their environment. Whole villages starved when the weather changed in unexpected ways so that they could not travel or when the game went "elsewhere." The people could not travel far enough into the tundra or out onto the ice to have access to all the habitat used by their game. Dominant groups occupied the more reliable sites. Subdominant groups were forced to look for new resources. One still hears stories of misery suffered among groups that had to travel off to new regions. The people developed a fatalistic philosophy of killing as much game as they could when the game was present and hoping to freeze and store it so that they did not starve before they got the next break from the capricious spirits. Older Eskimos will say that theirs is a hungry country and that anyone who practices conservation or sportsmanship will likely starve. Conservation of limited resources and prudence in cropping of game is irrelevant to people living on an island when 50,000 walrus drift past on the icepans in spring.

The Eskimos of the northwestern Bering Sea now kill walrus for the ivory. They carve the ivory and sell the carvings to tourists. They shoot walrus with high-powered rifles from aluminum boats with 50 h.p. outboard motors, yet the walrus hunt is still the major way a man can establish his identity. Now they eat some meat from a few of the first walrus shot and cut off the heads of the rest for the tusks. Headless carcasses of walrus littered the sandy beaches of the Seward Peninsula in 1975; we counted over 450 in the course of censusing for gulls. In the last few years the people have learned that

carcasses rotting on the beaches make bad public relations; they slit the bellies so the carcasses will not rot, bloat and float. The idea that they should make maximal use of any resource which they can seize is not a new idea which comes from association with the white man. A conservation ethic is simply foreign to them.

Although some native people did have a sophisticated and sympathetic land ethic, by no means all did. To suggest returning society's attitudes to those before "development" will be a form of "cop out" to avoid addressing the puzzling problems which we face.

Turning to our own economics, the market works, like natural selection, to satisfy selfish interests and to exploit, not to protect, resources. When a species becomes rarer, as have Polar Bears, the price rises and stimulates previously uneconomic search for more of that species until it (the supply) runs out. Pressures to meet short term goals inhibit or prevent attainment of long term optimization when the improvement requires a system to pass through temporarily nonadaptive conditions. The collapse of efficient public transportation in the face of selfish convenience of automobiles and the manipulation by big auto businesses illustrates the actions of the market in terms of the long range "public good".

Proponents of progress vociferously objected to the use of noise pollution and stratospheric contamination controlling the development of the Supersonic Transport; but now that economics (the aircraft are not paying for themselves) threatens to eliminate this symbol of technology, those voices are silent. Why does the profit motive still have the status of the golden calf? I suspect that many people see it as a mechanism that will divest society of the responsibility of making awkward decisions.

Our legislative/legal systems supply rules for another arena where selfish interests compete. No one of the special interests will yield its interests to the general good. For example, the discussions which led to the banning of pesticides were dominated by the power of special interests. Legislators required chemicals be available to all of the public or to none, because that is what the special interest groups demanded. The idea of restricted use in case of serious need was repugnant to those who did not trust the decision-makers. Each group insisted on defining "real need" themselves. So individuals in politics tend to manipulate legislative acts in their own interests, and it is the function of the courts to interpret those acts.

The courts play out their adversary proceedings according to an

esoteric set of rules which are interpreted by the specially initiated. Lawyers admit that ours is a patched-up system, but apologize that it is all we have. The adversary system will “beggar my neighbor,” as Harper says. If we espouse the adversary procedure, if we send our most eloquent and adamant proponent to the controversy, why are we surprised and annoyed when the opposition is also adamant and eloquent, — we say “intransigent”?

These pressures act on conservationists as well. The press of economic necessity pushes most conservation organizations to local concerns, because volunteers prefer to work in their own direct interests. Over time, some organizations have grown at the expense of others, primarily those have grown which are in effect insurance agencies for the environmental amenities of affluent suburbanites. The conservation organizations seem to respond first to politics as “fundamentalist institutions” — they brook little questioning of philosophical justification. Among conservation organizations as in the White House, scientific evidence is usually discarded if the science challenges political or economic “realities.”

A student of natural selection sees no contradiction in observing people and other animals or plants; their motivations are selfish. Our rules were patched on as our society outgrew the villages where everyone knew each other, knew everyone’s past behavior and could bring social pressure on antisocial individuals to conform to norms of the group (Trivers, 1971). Maybe our most serious problem results from the opportunities offered by anonymity.

A current flowing counter to selfishness has existed during the centuries. I think it makes humans special and gives us hope. It is a sense of responsibility. It can find biological roots in the actions of leaders who undertook some degree of “reciprocal altruism” (Trivers, 1971) for the larger group. This worked because the group gave loyalty and gratitude in return for care. In small in-breeding groups a sense of responsibility among the leaders on the one hand and of loyalty among the followers on the other increased “fitness.” This responsibility may have stretched beyond the extended family group when it was advantageous for several groups to join in hunting parties for big game of the Pleistocene. The story of human progress since then can, with some justification, be presented as an expansion of the group to whom we apply sense of responsibility, and I am sure that this idea is not new to me.

A major step in the neolithic revolution is domestication of stock

and cultivation of plants. This tremendous step requires assumption of responsibility for organisms which come to depend upon us and are not members of our own gene pool. There is good reason to believe that it was forced upon our distant ancestors when the mighty hunters of the late ice-age had exterminated the Pleistocene megafauna.

The Darwinian revolution challenged the easy confidence which people had had in the belief that humans are a special creation and in that ultimate arrogance "created in God's image." The social revolution which I see in the environmental movement gropes toward "internalizing" the implications of evolution in social thought. Now, if we are descended from apes, the question of who is my brother and who is my neighbor becomes even more awkward. If we feel free to pull up a wildflower which we call a weed in our garden, do we feel guilty to kill a Herring Gull which will drive Arctic Terns and Laughing Gulls from their nesting grounds? Do apes have special value? Do mammals? Do animals over plants? Does the philosophy of non-violence apply to mosquitoes?

We are committed to a debate among scientists, among conservationists, and among members of the public as to what we think is right for humans in their interactions with their habitat. Some would have natives kept as relicts of traditional ways of life. Similarly, some consider their responsibilities done when they have established wilderness where the affluent can enjoy their safaris or canoe trips. Are not those who are satisfied at setting aside sanctuaries in suburbia saying: "I'm all right Jack"?

We are now faced with a circumstance characteristic of many species of animals and plants: i.e., moving from one unsatisfactory and vulnerable adaptive peak (discredited theoretical base on contemporary ecological theory) to a defensible adaptive peak (valid theoretical justification) across a nonadaptive "valley" in which the ecological theory is considered invalid but the equally invalid market place and legal/legislative systems remain in force. We are disillusioned with our social institutions which act in the legal arena, the market place, or the legislatures. Yet those institutions are the stage upon which we must act and the ecological imperative is at present acceptable to important elements of society, including the courts and legislatures, although it may make an enlightened ecologist squirm.

This imperative may be essential to the many thoughtful people who are using whatever social institutions are available — political, legal, economic, endangered species act, restraining orders — to ensure that values which are not yet codified are not buried in the rush of economic expediency. we should wish them God's speed and should stiffen their resolve with scientifically valid support whenever we can.

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The material presented uses ideas from many directions, which, I believe, converge on the topic of the biology of rare species. My intent has been to present a set of insights which combine to form a picture of the lives of plants and animals in their world. These insights make up a way of thinking and serve the same function in the synthesis as do the spots of color by which an impressionist painter portrayed the atmosphere of a landscape. As such this work does not conform to expectations of the usual scientific paper in which a carefully delineated problem is identified and directly applicable evidence presented in a closely argued form.

Not surprisingly, the work upon which these ideas are based has had support from unusual sources. Most was through contracts to solve biological problems with pressing political implications. I would like to thank Dr. John Seubert, Animal Depredations Control Research, U.S. Fish and Wildlife Service for support for work on seagulls on the coast of New England; and Dr. David Norton, Arctic Project Office, Outer Continental Shelf Environmental Assessment Program of the National Oceanic and Atmospheric Administration for support for work on seabirds in the northern

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SUMMARY

Our perception of a species as rare implies a low frequency and a high intrinsic value. It has usually been assumed that a rare species is not successful and that it suffers from reduction of genetic variability or depauperization of habitat. These assumptions probably stem from deterministic models of community and species development. Contemporary studies of genetic polymorphism suggest that some small populations and some inbreeding populations retain heterozygosity. When one considers the density of species it appears that most species occur at low densities. A minority are numerous and another minority are endangered. At this stage it does not seem to help our understanding to assign a degree of success or failure to any species except in a specific context.

An operational definition of a rare species might include that its numbers are divided into subpopulations so that interbreeding is restricted or, in extreme cases, the species is reduced to a single population.

Plants have advantages for survival in small populations in that they can survive for long periods in vegetative form and do not seem driven to reproduce within a fixed life span. Plant reproduction seems to tolerate both more inbreeding and more hybridization than has been credited to active animals upon whose biology much ecological and conservation theory is based. Morphological plasticity, which is one important adaptation of plants, results in many cases in difficulty in identifying species boundaries, and in the extreme case the concept of an endangered species may need clarification.

Because each subpopulation will tend to have somewhat different genetic composition, one would expect that the number of subpopulations are more important for the persistence of a species than the total population size. Because isolation of an inbreeding population may encourage specialization and "conservatism," it may be that the first steps in rehabilitating an endangered species population is to break it up into largely, but not completely, independent populations. This policy is directly contradictory to the classical view of protectionists.

Plants have advantages for rehabilitation. Among them are the facts that many can readily be divided into clones, and that few botanists suffer humanistic pangs felt by animal lovers in removing competing species from the habitat or in expending large numbers of young in an attempt to establish a new station.

We are at an awkward transition in which the goals of the environmental movement are laudable but the justifications are often not valid scientifically because the models are deterministic and natural systems are not. Similarly deterministic models are the essence of the intellectual framework of our economic and legal institutions. It seems that these contemporary social institutions require outside intervention. Otherwise they provide opportunities for prostitution of human values to money and convenience or for a cop-out for those who do not want to address the conflicts between selfish interests and the long-term values. It was "irrational" political intervention in the *laissez-faire* policies of the 19th Century that protected landscape and endangered species, and there is little to convince us that anything else is the case today. Activists use whatever tools are available — endangered species act, restraining orders — and we should wish them God's speed even though many of the biological ideas they use make an enlightened ecologist squirm.

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